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# THE RUSTS OF CEREAL CROPS

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## INTRODUCTION

No plant pests have been more detrimental to man's welfare and progress than the cereal rusts, 11 kinds of which are now known. Intermittently for many centuries one group of these rusts, the wheat rusts, have taken enormous toll from farmers' incomes, and, at times, have seriously threatened man's food supply.

Much has been published concerning the rusts, but it was not until near the middle of the eighteenth century that it was discovered that they were fungi. Prior to that time there were various popular beliefs as to the cause of rust, chief among which was one held by the Romans, which attributed the periodic ravages of the scourge to a special rust god, Robigus, who resorted to this means of wreaking his vengeance on a wicked people. Another and more persistent belief, one that prevails here and there even to this day, attributes rust solely to the weather. We now know that weather greatly affects the development and spread of rust; we know also that there can be no rust without the causative fungus, a parasitic plant that finds its way into the tissues of a plant and draws its sustenance from them, thereby materially injuring the plant.

The rusts here considered are, according to their hosts, or the plants they grow on, as follows: Wheat—stem rust (*Puccinia graminis tritici*), leaf rust (*P. triticina*), stripe rust (*P. glumarum*); oats—stem rust (*P. graminis avenae*) and crown rust (*P. coronata*); barley—stem rust (*P. graminis tritici*) and leaf rust (*P. anomala*); rye—stem rust (*P. graminis secalis*) and leaf rust (*P. dispersa*);

corn—corn rust (*P. sorghi*); and sorghum—sorghum rust (*P. purpurea*). Many of these rust fungi, notably those causing stem rust, crown rust, and stripe rust, parasitize also numerous wild and cultivated grasses. All of the cereal rusts, except stripe rust and sorghum rust, spend a part of their life cycles on some plant other than their cereal or grass hosts. In the case of stem rust this alternate host is the common barberry; for crown rust it is the buckthorn, chiefly. It is on the alternate host that the cluster-cup spores (aeciospores) form and from it that they are discharged. The life cycles of the cereal rusts that are characterized by an alternate host are essentially alike, as will be noted on glancing at the life-cycle diagrams accompanying the text.

Many of the cereal rusts have become considerably specialized into varieties or strains, each variety being characterized by its host preference or preferences. For example, we now recognize several varieties of stem rust, one peculiar to rye and certain wild grasses, another to wheat and certain other grasses, a third to oats, and so on. The same is true also of crown rust and stripe rust. Then, again, within each variety we find further and more restricted specialization in which the variety may contain from two to many parasitic strains (physiologic forms), each strain having its preferences, its congenial hosts, within the particular kind of cereal crop to which it is peculiar.

The distribution of the cereal rusts is, in general, coextensive with that of the cereals and grasses they attack. Stem rust of wheat, for example, occurs in every part of the world where wheat is grown. The same is also true of leaf rust of wheat and crown rust of oats. While it often happens that these and the other rusts cause little or no loss to the grower, occasionally their ravages are enormous. As an illustration, it is only necessary to cite the terrific damage wrought by stem rust in 1916, when the farmers of Minnesota, North Dakota, South Dakota, and Montana suffered a loss of 180,000,000 bushels of wheat. Not a year passes but all of the rusts together exact an important toll from the world granary and cause notable fluctuations in yields.

There is no known method by means of which any of the cereal rusts can be entirely prevented. Much, however, can be accomplished in their control by the destruction of the alternate hosts, notably the common barberry and the buckthorn. Strains and varieties that are highly resistant to the rust or rusts peculiar to the crop concerned also may be produced through breeding and selection. Control by dusting with sulphur or other fungicides has been experimentally successful, but the use of this method on a commercial scale has not been practicable.

## WHEAT RUSTS

### STEM RUST[1]

**Description.**—Stem rust of wheat, as well as each of the other cereal rusts, is caused by a tiny, parasitic moldlike fungus.

Stem rust may attack all aboveground parts of wheat plants: The leaves, leaf sheaths, stems, glumes, beards, and sometimes the kernels. During its life on the wheat plant the rust fungus com-

[1] *Puccinia graminis tritici* Eriks. and Henn.

monly has two distinct stages—the red (uredial) and the black (telial), sometimes called also the summer and the winter stages.

The red stage appears in the spring or summer and produces long-ish, brick-red rust pustules or uredia, which may appear on all parts of the plants except the roots. They are, however, most conspicuous on the stems; hence the name stem rust. The pustules break through the epidermis of the plant, giving it a torn, ragged appearance. The number and size of pustules vary with the variety of wheat, with the severity of rust attack, and with weather conditions, but their dark-red color and the way in which they tear the epidermis of the plant enable a person to distinguish stem rust from the other wheat rusts.

The pustules are filled with a brick-red dust (urediospores) that looks somewhat like iron rust; hence the name. When heavily rusted wheat is being cut, this dust may rise like a fog and cover the harvesting machines, horses, and men working in the field. Often, however, the red stage is largely replaced by the black stage shortly before harvest.

Conditions unfavorable for the development of the red stage usually bring on the black stage. In hot, dry weather the uredia may gradually become brownish black, while the wheat plants are still relatively green. Usually, however, the black stage begins to appear when the wheat starts to ripen; but, if it ripens quickly, very few telia may appear. Their size and shape are about the same as those of the uredia, but the telia are not powdery and, instead of being brick-red, they are brownish black or dull black.

**Plants attacked by stem rust.**—All classes of wheat, durum, spelt, emmer, and einkorn, are more or less susceptible to stem rust, although some varieties in most of the classes are far more resistant than others. Barley, also, is as readily attacked as wheat, and rye sometimes may be attacked lightly. Stem rust develops normally also on many wild grasses, especially the wild barleys or squirreltail grasses, *Hordeum* spp.; western wheatgrass, slender wheatgrass, and closely related kinds, *Agropyron* spp.; the wild ryegrasses, *Elymus* spp., bottlebrush grasses, *Hystrix* spp.; and some of the bromegrasses, *Bromus* spp.; as well as many less well-known grasses. Strangely enough, the wheat variety of stem rust does not attack oats, nor does it develop well on quackgrass, *Agropyron repens* (L.) Beauv., although it infects severely some of its near relatives. Stem rust on barley and the wild grasses has the same appearance as that on wheat, and the rust can pass freely from one kind of grain or grass to another within the general group mentioned above.

The uredial and telial stages of stem rust develop, therefore, on wheat, barley, and many wild grasses. There is another stage, the spring or cluster-cup stage, which appears on certain kinds of barberries, as described on page 5.

**Life history.**—Stem rust consists of a much-branched growth (thallus) of very slender, almost colorless tubes (hyphae), so small that they can be seen only when greatly magnified. Each branch or tube is called a hypha. These hyphae grow into the tissues of the cereal host plant (wheat, oats, barley, or rye) and obtain from them food necessary to the proper growth and maturity of the host. Hyphal masses finally form under the epidermis and produce numerous red spores (urediospores). The enlarging spores rupture the epidermis and form the pustules (uredia), which are filled with urediospores.

The stem-rust fungus multiplies and reproduces by means of these spores propagative bodies that in a general way are similar to but much simpler than the seeds of higher plants.

The urediospores of stem rust are approximately 0.03 millimeter long and are produced in prodigious numbers. As they are so small and light, countless billions of them are blown about by the wind and may fall on grain or grass plants, germinate there in drops of dew or rain water, and subsequently cause new infections.

The time required for the spores to germinate depends on moisture and temperature. They germinate quickly when it is warm and more slowly when it is cool. At a temperature of 40° to 50° F. several hours may be necessary, but at about 75° they may germinate within an hour, and, by means of their tubes, promptly enter the wheat plant.

Spore germination can be observed easily under the microscope. Each spore produces one or two germ tubes that grow along the surface of the plant until they reach a breathing pore (stoma), where they enter, send out branches that grow through the tissues of the plant, draw nourishment from them, and keep on growing and branching for a week or longer, until they have formed an extensive network or mycelium, which proceeds at once to produce another crop of spores. At low temperatures, or when there is but little sunlight, it may take 2 or 3 weeks from the time the germ tube first entered the plant for spores to form; in warm, moist weather, however, they may reach full development within a week. Naturally, then, rust spreads faster when the weather is warm and moist than when it is cool and dry.

The black spores (teliospores) will not germinate immediately after they are formed but require a relatively long resting period, somewhat like the hard seeds of alfalfa and clover. They are not blown about by the wind, but remain on straw or stubble throughout the winter and germinate in the spring, especially in moist, cool weather. On germination, they produce small colorless spores (sporidia) that germinate and readily infect certain species of barberry.

It is an extremely important fact that the winter spores do not cause infection and that their sporidia cannot infect grains or grasses but infect only the barberry.

The sporidia germinate on barberry leaves and send out small germ tubes that penetrate the epidermis directly; hence, only young parts of the plant can be infected, for the germ tubes cannot penetrate the older, tougher parts.

Within a week or 10 days after germ tubes of the sporidia have entered the barberry, small yellowish or honey-colored spots appear on the infected portions, especially the young leaves. These yellow spots comprise the spermogonia, which contain the spermatia. These latter function in connection with the sexual reproduction of the rust. Within a short time the cluster cups (aecia) are produced, commonly on the under surface of the infected leaf. These small cup-shaped structures contain long chains of cluster-cup spores (aeciospores). These spores are shot forcibly from their cups, especially during moist weather, are blown about by the wind, and initiate the red or summer stage of the rust on grains or grasses.

The typical life history (fig. 1) of stem rust is, then, as follows: The rust overwinters in the black or teliospore stage; the teliospores germinate in the spring and produce sporidia, which cannot infect grains and grasses but do infect certain kinds of barberries, on which the aecial stage subsequently develops. The aeciospores cannot infect the barberry but, falling upon grains and grasses, germinate and induce the uredial stage. This stage may persist and pro-

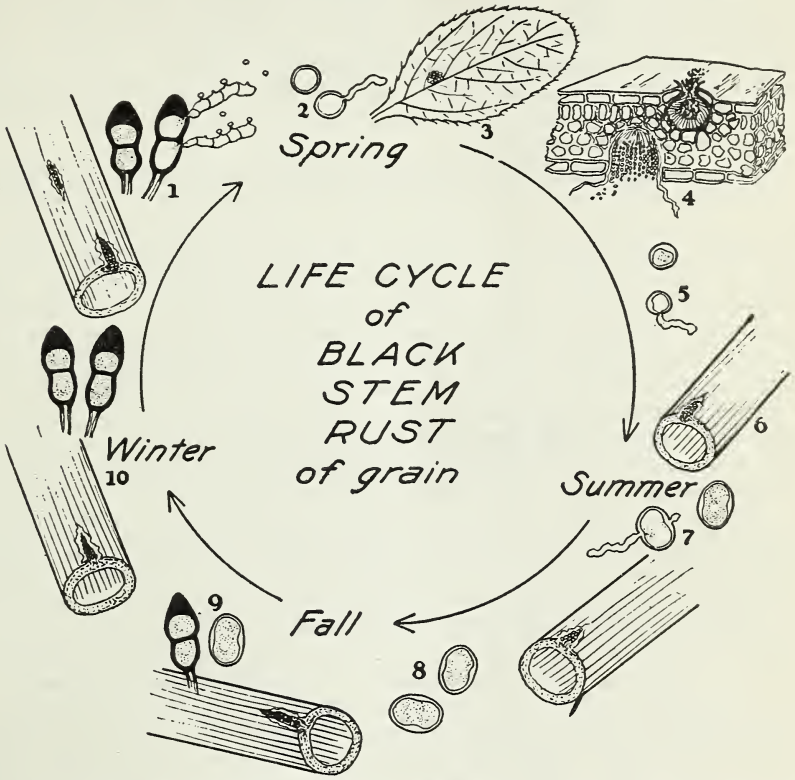


FIGURE 1.—Life cycle of stem rust of wheat, oats, barley, and rye: Overwintering black spores (teliospores) germinate (1) in the spring. They produce several very small spores (basidiospores) (2) that are carried by air currents to nearby barberry bushes, where they germinate. The resulting infection of the barberry (3) produces spermogonia and cluster cups (aecia) (4). Cluster-cup spores (aeciospores) are blown to grainfields and germinate on the grain plants (5), where they produce rust-infection pustules on the stems and leaves (6). These pustules contain the red or summer spores (urediospores) (7), which reinfect the crop, producing more of their kind (8), until toward the end of the growing season, when the black-spore pustules develop and the teliospores (9) mature and spend the winter on straw and stubble (10), where they germinate in the spring.

duce successive crops of urediospores until growing conditions become unfavorable, when the teliospores are produced.

While the stem-rust fungus actually produces five kinds of spores, only the urediospores and aeciospores can infect grains and grasses. The teliospores, by means of which the rust usually survives the winter, are harmless unless there are barberries nearby. If this typical life cycle were always followed, there would, then, be no stem rust without barberries. The only other way in which rust could

perpetuate itself would be through urediospores that had survived the winter.

**Parasitic strains.**—Over a hundred distinct parasitic strains or physiologic forms of the stem rust of wheat have been discovered, more than 50 of which occur in the United States. They differ in their ability to attack certain varieties of wheat. For example, some attack the variety Marquis but not Kanred; others attack Kanred but not Marquis. Still others attack certain varieties of bread wheat but not the durums. Others can attack the durums but do not develop normally on the bread wheats. The durums are resistant to many parasitic strains and usually suffer little injury. But, in 1923, 1927, and 1932, they were badly rusted in the Dakotas, especially in North Dakota, as strains of the rust were present that were capable of attacking durum wheat.

The same parasitic strains are not always present in a given region in different years, and there may be different strains in several regions in the same year. For this reason a variety may be susceptible to rust in one region and resistant in another, and it may be susceptible in a given region in certain years and resistant in others. The development of stem rust on wheat, then, depends not only on the presence of numerous spores early in the growing season but also on the presence of spores of the particular parasitic strains that, normally, can attack the variety of wheat grown in that region.

**Development of epidemics.**—The first requisite for the development of a rust epidemic is a large number of spores early in the growing season. In the Northern States tremendous numbers of spores usually are produced on barberry bushes before the middle of May. As many as 70 billion aeciospores may be produced on a single moderately large bush, and each spore can, if the weather is favorable, bring about the formation of a pustule of the uredial stage on grains or grasses within a week or 10 days. In each one of these pustules there may be upwards of 350,000 urediospores. Clearly, then, a single barberry bush, under ideal conditions, can cause a prodigious amount of rust. Because of this important role played by the barberry in the propagation and spread of stem rust, there has been in progress since 1918 a campaign of barberry eradication in Colorado, Illinois, Indiana, Iowa, Michigan, Minnesota, Montana, Nebraska, North Dakota, Ohio, South Dakota, Wisconsin, and Wyoming, where there were millions of barberry bushes. More than 18 million of these have been destroyed. The effect is already apparent in reduced amounts of stem rust, although millions of bushes still remain to be destroyed.

The distance that rust may spread from barberry bushes depends on weather conditions. Very often local epidemics extend from half a mile to 5 miles from the bushes, but, under favorable conditions, the rust may spread much farther. For example, in south-central Minnesota, several years ago, rust had spread 10 miles from a barberry hedge by the first week in July. It could not be traced farther because it was then uniting with local epidemics arising from other bushes.[2]

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[2] For further details see the following publication: Stakman, E. C., Kempton, F. E., and Hutton, L. D. THE COMMON BARBERRY AND BLACK STEM RUST. U. S. Dept. Agr. Farmers' Bull. 1544, 29 pp., illus. 1927. (Revised, 1930, by E. C. Stakman and D. G. Fletcher.)

In the Southern States rust seldom develops on barberry bushes because the black spores, or teliospores, are formed in May or early June and cannot survive the long hot summers. Urediospores, however, are produced continually throughout the year, and the life of the rust is, therefore, independent of the barberries in those States and in California, Oregon, and Washington.

When weather conditions favor the winter survival of urediospores in the South and spring conditions there favor rapid development of the rust, strong overland south winds blowing for several days during the first half of June may carry rust spores northward and infect grainfields in the Northern States. If the weather is then warm and moist, epidemics may develop independently of the barberry, particularly in the spring-wheat region.

Even when there are many spores early in the spring, epidemics do not always result. There are two principal reasons for this: (1) Weather conditions are not always favorable for rust development; and (2) some wheat varieties are resistant to many parasitic strains of the stem-rust fungus.

There is always a race, then, between the rust and the wheat. If the wheat can ripen before the rust has had a chance to produce several crops of summer spores, it may escape damage. If, on the other hand, the weather is warm and moist enough to permit very rapid multiplication of the rust, it is likely to injure the wheat severely before it ripens or even prevent it from ripening normally. There is a tendency for stem-rust epidemics, therefore, to develop in those years when the temperature is somewhat higher than the average during the growing season, provided it is not too dry; whereas, in years in which the temperature is lower than the average, stem rust seldom does much damage. Sometimes heavy rust epidemics may develop in cool seasons, when one would not expect them, merely because cool weather may retard the ripening of wheat more than it retards the development of rust. Again, because of insufficient moisture, rust may not become destructive in abnormally hot seasons.

**Distribution and economic importance.**—Stem rust is more or less abundant wherever susceptible varieties of wheat are grown in the United States, but it is more destructive in the spring-wheat area of eastern Montana, the Dakotas, and Minnesota. Because winter wheats ripen earlier than spring wheats, they usually escape severe rust injury, although damage sometimes occurs in the hard red winter and in the soft red winter wheat areas. In eastern Oregon and Washington and in northern Idaho stem rust is unimportant, and in California the conditions are so varied that rust usually is important only locally. The losses from rust in the United States have decreased considerably since the barberry-eradication campaign was begun.[3]

**Control.**—While stem rust cannot be eliminated completely, the combination of the following methods can be depended on to reduce losses very greatly: (1) Proper selection, preparation, and fertilization of the land; (2) the use of early maturing or resistant varieties; (3) dusting, particularly valuable stands of wheat, with sulphur dust; and (4) complete destruction of the common barberry, to pre-

[3] Stakman, E. C., Kempton F. E., and Hutton, L. D. See footnote 2.

vent the early development of rust in the Northern States and to prevent the production of new physiologic forms.

**Cultural practices.**—Where stem rust is likely to be destructive, land should be carefully selected and prepared. It is best to sow wheat on fairly high land, where there is good air drainage, rather than in hollows and pockets, where the plants remain wet with dew or rain and thus give the rust a good opportunity to cause infection. Anything that is likely to hasten the maturity of wheat may reduce the amount of rust. Early seeding on well-prepared soil often works to the advantage of spring wheat. The application of proper fertilizers sometimes aids in reducing damage from rust. The use of too much barnyard manure or excessive use of nitrogenous fertilizers of any kind should be avoided. Too much nitrogen may cause heavy stands and late ripening, and thus give the rust a better and longer opportunity to develop. The application of phosphorus and potash to those soils that need them, often promotes the development of a good root system, stiff straw, and early ripening, and thus reduces the damage from rust. The real test of the value of fertilizers, of course, is their effect on yield and quality, but intelligent use of fertilizers often assists in reducing the amount of rust.

**Early maturing varieties.**—The use of early maturing varieties is sometimes extremely valuable in reducing rust damage. This is particularly true in the spring-wheat region of the upper Mississippi Valley. Such early varieties as Prelude, Ruby, and others sometimes escape severe rust injury, while later varieties are badly damaged. However, varieties are not likely to be grown merely because of their earliness unless they have other desirable characters.

**Resistant varieties.**—For more than 25 years the United States Department of Agriculture, in cooperation with various State experiment stations, has been attempting to develop rust-resistant varieties of wheat, and gratifying progress has been made. At one time it was thought that the many parasitic strains of stem rust might make it impossible to develop generally resistant varieties. It has been found recently, however, that certain varieties are generally resistant in the field wherever they are grown. Of the spring wheats, Marquillo and Ceres are resistant and are now rather widely grown. Breeding work now in progress promises the development of still better varieties than these. Many varieties of durum wheat have been resistant in most years and in most localities in the durum-growing regions. Sometimes, however, when virulent parasitic strains of the rust are present and the weather conditions are favorable, both the durum and common wheats may be severely injured. Of the hard red winter wheats, Kanred seems to have considerable value because of its relative rust resistance. It rusts in some years and in some places, depending on the parasitic strains present, but its record over a period of years shows clearly its value as a rust-resistant wheat.

The question is often asked whether resistant varieties of wheat will retain their resistance. Varietal resistance is as constant as other characters. But it is true that certain varieties have been resistant for a time and then have seemed to become susceptible. This is explained by the fact that new parasitic strains of rust sometimes appear where they have not occurred previously. Under such circumstances, the variety might seem to have lost its resistance; but,

in fact, it has not lost its resistance, but has merely been exposed to a parasitic strain to which it is not resistant. While varieties like Marquillo and Ceres, especially the latter, may sometimes develop a moderate amount of infection, their performance thus far indicates that they are far more resistant than ordinary varieties, that they yield better in rust years, and that they may long remain resistant. Through breeding and selection, hybrid varieties obtained from crosses between such varieties as Hope and Ceres, Hope and Marquis, and Pentad and Marquis can be obtained in which a high degree of rust resistance, satisfactory agronomic characters, and excellent milling and baking qualities may be combined.

**Dusting with sulphur.**—It has been shown in recent years that stem rust can be controlled by dusting the growing crop with a suitable sulphur dust, provided the application is made properly and at the right time. In order to control rust profitably, it would be necessary to make the first application of dust about the time the plants are heading and subsequent dustings at intervals of a week until just before harvest. In order to protect fairly large fields, a power duster, costing between $400 and $500, would be necessary. It is not yet known definitely whether in an average crop year it would pay a farmer to dust his wheat. Much, of course, depends on the price of wheat and on the severity of rust attack. In years when the price is fairly high and rust does a great deal of damage, it undoubtedly would pay. When, however, the price of wheat is low and rust is not destructive, it would not pay. Whether it would be profitable over a period of 8 or 10 years has not yet been determined. Even under present conditions, however, it may be advisable for growers of pure seed of particularly valuable varieties to dust.

**Barberry eradication.**—All rust-susceptible barberries should be eradicated from the grain-growing regions of the Northern States. Observations and experiments, covering many years, have shown clearly that in some regions the only destructive outbreaks of rust occur near barberries, while in other regions the barberry is a very important contributing factor in the development of rust (fig. 2). Furthermore, it is evident that the severity and frequency of rust attacks have decreased with the progressive decrease of rust-susceptible barberries. It has been shown also that new parasitic strains of rust are produced by hybridization on the barberry.[4]

## LEAF RUST[5]

**Description.**—The leaf rust (orange leaf rust, brown rust) of wheat usually attacks the leaf blades and sheaths, although it may sometimes occur on the stem proper, especially just below the heads. Sometimes it occurs also on the chaff and awns or beards. The rust pustules are smaller than those of stem rust, are more nearly round, and are less likely to unite. Usually they appear only on the upper side of the leaf. The color of the red or summer (uredial) stage is orange to orange-brown, being brighter than that of pustules of stem rust. The pustules of the black or winter stage (telial) are of about the same size as those of the red stage, but they seldom break

[4] Stakman, E. C., Kempton, F. E., and Hutton, L. D. See footnote 2.
[5] *Puccinia triticina* Eriks.

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through the epidermis of the plant, and the color, therefore, is likely to be lead-gray. The cluster-cup or spring stage (aecial stage) does not occur to any extent in nature in the United States.

FIGURE 2.—*A*, The most practical and effective herbicide for barberry destruction is common salt. It is applied in generous quantity at the base of the plant where, on being dissolved by rain and melting snow, it enters the soil and kills the roots. *B*, Several barberry bushes that have been killed by salt.

There are several rusts on other cereals and on wild grasses that look very much like the leaf rust of wheat, but they do not attack wheat to any extent.

**Distribution and economic importance.**—Leaf rust of wheat is found almost wherever wheat is grown. In the United States it is

most abundant and destructive in the Southeastern States and in the Ohio and Mississippi Valleys, where weather conditions usually are most favorable for its development. It is less destructive in the hard red winter and the hard red spring wheat areas, although it is usually present to some extent and in favorable seasons may cause considerable damage to certain varieties. In the irrigated areas of the West and on the Pacific coast it usually is present but seldom

FIGURE 3.—The head and kernels to the left of the median line are from a rust-free plant; those on the right are from a rusted plant. Leaf rust of wheat seldom shrivels the kernels, but it does reduce their size, number, and quality.

does extensive damage, although sometimes it may be of importance locally (fig. 3).

Leaf rust may cause much damage to certain varieties of wheat in certain regions, although the damage is less conspicuous than that caused by stem rust. Leaf rust seldom shrivels the kernels, but it does reduce their size and number and the quality of the grain. Furthermore, when plants become heavily rusted while still young, the entire plant may be weakened and somewhat dwarfed, and, under such circumstances, the yield may be reduced as much as 90 percent.

According to estimates of the Plant Disease Survey, United States Department of Agriculture, the total reduction in yield caused by leaf rust in the United States during the 9-year period 1919–27 was 108,380,000 bushels, or an average of 12,042,000 bushels a year.

**Plants attacked by leaf rust.**—The only common small grain on which leaf rust of wheat develops is wheat. Among the wild grasses it finds no congenial hosts, except a few species of goatgrass, which are somewhat susceptible. It may, occasionally, attack barley to a slight extent, but for practical purposes it may be considered as attacking wheat only. The cluster-cup stage of leaf rust occurs on certain species of meadowrue (*Thalictrum*), but this is of no practical importance in the United States, as the species that are native here do not become infected under natural conditions.

**Parasitic strains.**—There are many parasitic strains of the leaf rust of wheat that differ in their ability to attack different varieties. More than 50 of these strains have been identified in the United States. It is very probable that more will be discovered, as there is evidence that new ones are occasionally coming into existence. The exact manner in which they originate, however, is not known.

**Life history.**—Leaf rust of wheat, like all other rusts, is caused by a very small parasitic fungus that enters the wheat plant through its breathing pores, or stomata (fig. 4).

The complete life cycle of leaf rust of wheat is similar to that of stem rust, except that the cluster-cup stage develops on species of meadowrue instead of on barberry. On wheat the red or summer stage continues as long as the wheat plants are green and growing. The red or orange-colored pustules (uredia) that develop on the wheat contain thousands of red or summer spores (urediospores), which are easily blown about by the wind and are capable of causing rust on other wheat plants, after they germinate and send their germ tubes into the plants. During warm, moist weather, this red or summer stage may recur every week, thus enabling the rust to increase and spread very rapidly. When conditions become unfavorable for the growth of the wheat and for the development of the red stage, the black or telial stage appears. In this stage the rust survives the winter and is capable of attacking species of meadowrue in the spring, on which the cluster-cup or aecial stage of the rust is formed. As already mentioned, however, the species of meadowrue commonly occurring in the United States do not become infected in nature, and the black stage and the cluster-cup or spring stage are of no importance in the persistence and development of the rust in this country.

The red or summer stage of the rust is capable of surviving the winter in most of the wheat-growing regions of the United States. It can be found at all times of the year in the Southern States and, in some years, in the Northern States. If weather conditions in late summer and early fall favor rust development, that is, if there is considerable moisture, the red stage attacks volunteer wheat plants and fall-sown wheat, where it may remain and even increase somewhat during the winter. When the winter is fairly mild and there is not too much alternate freezing and thawing, and when there is a fairly good snow cover, the rust may overwinter in considerable quantities over large areas. In the spring it then increases rapidly if weather conditions are favorable. The spores may then be carried

long distances by the wind and infect wheat plants in regions where the rust may not have survived the winter.

**Development of epidemics.**—As with other rusts, the first essential for the development of a leaf-rust epidemic is an abundant supply of spores in the spring. It has already been pointed out that there usually are enough spores in many regions to start an epidemic under favorable weather conditions. The destructiveness of the epidemic will depend on the earliness with which plants are attacked in the spring.

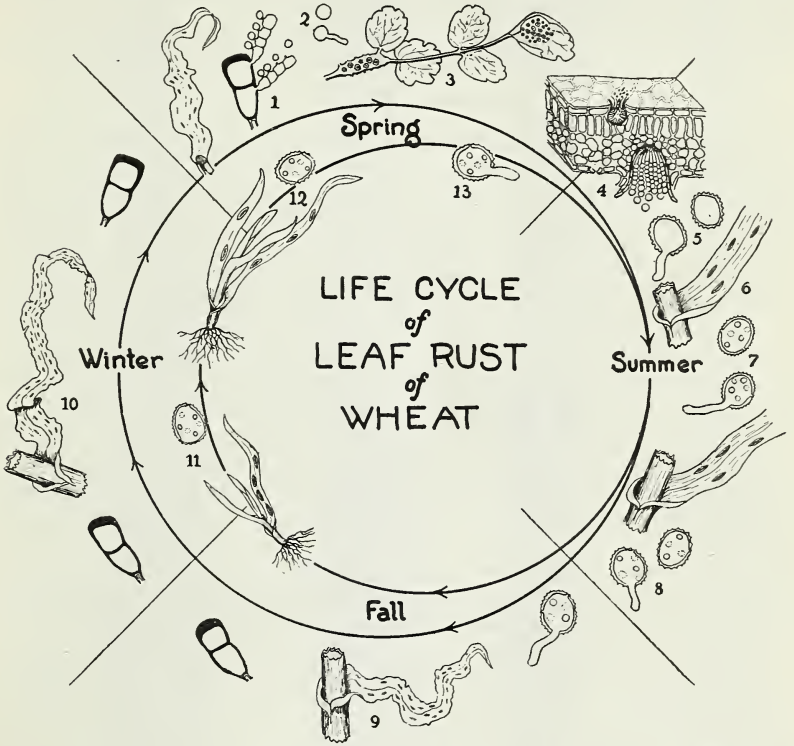


FIGURE 4.—Life cycle of leaf rust of wheat: Overwintering black spores (teliospores) germinate (1) in the spring, producing basidiospores (2), which blow to meadowrue (3), germinate, and produce infection from which spermogonia and cluster cups (aecia) (4) are produced. The cluster-cup spores (aeciospores) lodge on wheat plants and germinate there (5), producing infection from which the summer-spore pustules (uredia) arise. The summer spores (urediospores) thus produced repeatedly reinfect wheat, producing other uredia and urediospores (8). Finally, when the crop is nearly ripe, the black or winter spores (teliospores) (9) appear. These overwinter on wheat litter (10) and germinate in the spring (1). In the winter-wheat areas urediospores infect volunteer wheat (11) and survive the winter, and the resultant rust may then produce uredia (12) in the spring, and the urediospores (13) reinfect the growing wheat.

When there is abundant rainfall or heavy dews in the spring and early summer, following a winter that has favored the survival of the red stage of the rust, abundant early infection may occur. If the weather continues warm and moist, there is danger of a destructive epidemic. As in the case of stem rust, warm, moist weather is most favorable for the development of leaf rust, but this rust seems able to develop under a wider range of conditions than does stem rust; hence, severe attacks are more likely to occur over wide areas.

**Control.**—The practices mentioned under stem rust will aid somewhat in reducing the amount of leaf rust but cannot be depended upon to control it entirely.

Some varieties of wheat are more susceptible to leaf rust than others. Most durum varieties are highly resistant. None of the commercially desirable wheats so far known is resistant to all parasitic strains of this rust. The problem, therefore, is to breed varieties that combine desirable commercial characters with rust resistance. Such work is in progress and may be expected to contribute materially to the solution of the leaf-rust problem.

This rust can be controlled by dusting with sulphur, but this method of prevention is too expensive to justify its general use.

### STRIPE RUST [6]

**Description.**—Stripe rust has been commonly known as yellow rust because of the yellow or orange-yellow pustules of the summer stage. Stripe rust seems a better name, however, because one of the most characteristic features of the rust is that the pustules are arranged in rows of varying length, giving the appearance of fairly narrow yellow stripes. Stripe rust develops most abundantly on the glumes or chaff, on the leaves, and on the leaf sheaths, but it may also attack the stems and even the kernels. Its yellow color and stripelike appearance are quite characteristic. On seedling plants, and sometimes even on older plants, the stripes are not distinct, but the yellow color distinguishes the rust from other cereal rusts (figs. 5 and 6).

If the attack of stripe rust is heavy, especially on the necks and glumes, considerable damage is likely to result, particularly if plants have become rusted during the milk stage or earlier. Under such conditions the kernels may be shriveled and the yields considerably reduced.

The black stage of the rust may develop at any time during the growing season and at any stage in the development of the host. As in other cereal rusts, the black stage is formed after the red or summer stage. The black pustules (telia) also are produced more or less in rows, giving the appearance of long, narrow, dark-brown or black stripes. They may appear on all aboveground parts of the plant, including even the kernels.

**Distribution.**—In many regions of Europe, stripe rust is the commonest and most destructive grain rust. It has been reported also from certain countries of Africa and South America, and from Japan, China, and India.

In the United States, stripe rust was first discovered in 1915 near Sacaton, Ariz., although it was later found that it had been present in the Pacific Northwest certainly since 1892. It has been observed as far east as the Black Hills in the United States and still farther east, in Saskatchewan, Canada. As far as is now known, its distrbution in North America is restricted to Arizona, California, Colorado, Idaho, Montana, Oregon, western South Dakota, Utah, Washington, and Wyoming, in the United States; and Alberta, British Columbia, and Saskatchewan, in Canada; and Mexico.

**Parasitic strains.**—There are two principal parasitic varieties in North America. One of them attacks wheat, barley, rye, and a large

[6] *Puccinia glumarum* (Schm.) Eriks. and Henn.

number of wild and cultivated grasses; the other, apparently, is restricted to a species of wild barley, *Hordeum murinum* L., on the Pacific coast. The first variety comprises a number of parasitic strains, which differ in their ability to attack certain varieties of wheat and possibly other hosts. Doubtless other strains will be dis-

FIGURE 5.—*A*, Leaves of wheat infected with stripe rust (*Puccinia glumarum*), showing the long, characteristic stripes caused by the rust pustules and the underlying leaf tissue killed by the rust fungus; *B*, leaves of wheat infected with leaf rust (*P. triticina*).

covered, as investigation of this phase of the problem has been under way for only a relatively short time.

**Plants attacked.**—Stripe rust attacks wheat, barley, rye, spelt, emmer, and more than 60 species of wild and cultivated grasses. In the United States it is most prevalent on wheat and certain wild grasses and is seldom found on barley and very rarely on rye. It is espe-

cially common on some of the wild barleys and bromegrasses and on a species of goatgrass.

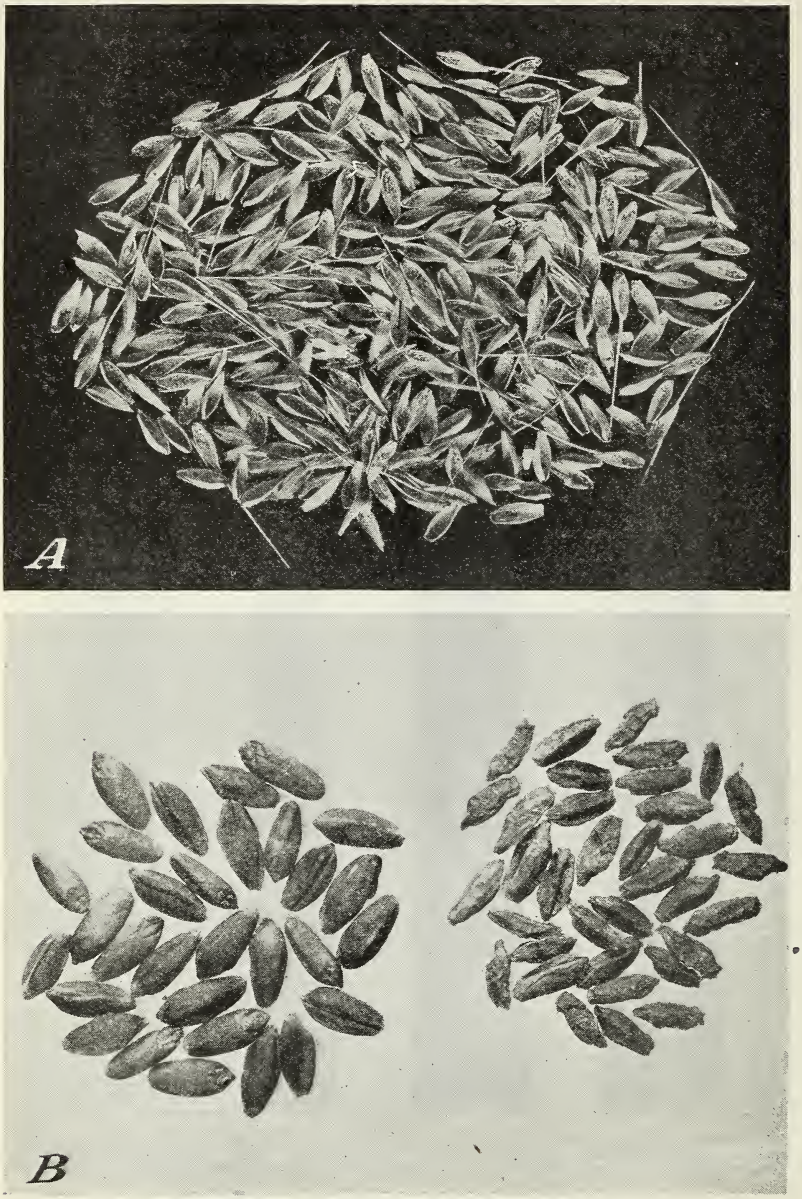


FIGURE 6.—*A*, Chaff of Chul wheat heavily infected with stripe rust. *B*, Two lots of kernels of Chul wheat: Left, from rust-free plants; right, from severely rusted plants.

**Life history.**—Both the summer or yellow-spore stage and the black stage of stripe rust are produced in the United States. But the black stage is not yet known to attack an alternate host; therefore, the cluster-cup (aecial) stage is unknown. The entire life his-

tory, for practical purposes, is, therefore, in the yellow or summer stage. The exact conditions under which this stage overwinters most abundantly are not yet known, although it is known to persist throughout the winter under a variety of climatic conditions.

**Development of epidemics.**—Epidemics of stripe rust are most likely to occur when there has been abundant infection in late summer and fall of the previous year, when a large number of summer spores and abundant mycelium have survived the winter, and when spring and summer conditions, such as cool nights, warm days, heavy dews, and abundant sunshine prevail during the growing season. The exact weather conditions under which stripe rust develops best are not known, but apparently moderate temperatures and abundant moisture are most important. Unlike some of the other cereal rusts, stripe rust seems to thrive best at low temperatures; in fact, its development is likely to be checked by hot weather.

**Economic importance.**—While stripe rust is extremely destructive in some foreign countries, it has caused relatively little damage in the United States, except in limited areas where susceptible varieties are grown and where weather conditions are very favorable.

Stripe rust has not become established in the principal grain-growing regions of the Mississippi Valley. How destructive it might be in those regions, therefore, is not known. From experience in other countries, however, it seems likely that it might be very destructive to some varieties of wheat under favorable weather conditions.

When the upper portion of the stems, the chaff, and the kernels become rusted during the milk or early dough stage of kernel development, the grain may be considerably shriveled. This results in smaller yields and wheat of inferior grade and quality. Badly rusted grain may germinate poorly, but it is incapable of transmitting infection to plants grown from such diseased seed.

**Control.**—Stripe rust can be controlled by the use of resistant varieties. Resistant varieties are available in those regions where it occurs, and destructive outbreaks occur only on susceptible varieties, which need not be grown. Although resistant varieties are available, the breeding of superior, new varieties is also desirable.

## OAT RUSTS

### STEM RUST [7]

**Description.**—The appearance of stem rust on oats is similar to that on wheat. Stem rust can be distinguished from crown rust by its darker color and by the fact that it usually produces longer pustules and is more abundant on the necks of the plants. The color of the summer stage of stem rust usually is brick-red, whereas that of crown rust is a bright yellow.

**Life history.**—Of the common small grains, the stem rust of oats attacks only oats. It attacks a number of the wild grasses also, including particularly orchard grass, some of the fescue grasses, meadow foxtail, and bluejoint. Normally it does not attack wheat, barley, or rye. Otherwise, the life history of this rust is the same as that of stem rust of wheat.

[7] *Puccinia graminis avenae* Eriks. and Henn.

Epidemiology.—Essentially the same as that of stem rust of wheat (p. 6).

Control.—Control measures for stem rust of oats are the same as those for stem rust of wheat (p. 7). There are a number of resistant varieties of oats, especially Richland, Iogold, Anthony, Rainbow, Minrus, White Tartar, and Green Mountain.

### CROWN RUST[8]

Description.—Crown rust of oats, often known also as leaf rust or orange leaf rust of oats, occurs principally on the leaves, although it is frequently present also on the leaf sheaths and sometimes on the stems and panicles. As with the other rusts, there are two stages on the cereal crop, the red or summer stage and the black or winter stage. The pustules (uredia) of the red or summer stage are usually more or less circular, although some of them are much longer than wide. The number and size of pustules vary a great deal, depending on the susceptibility of the host, the part attacked, and the severity of the infection. The pustules of the summer stage rupture the epidermis just as do those of stem rust. The color is orange-yellow, which makes it possible to distinguish this rust from the corresponding stage of stem rust. Later in the season the black or winter stage appears. These black pustules usually do not rupture the epidermis but remain under it, as in the case of the leaf rust and stripe rust of wheat. The cluster-cup stage of crown rust develops on a number of species of buckthorn (*Rhamnus*). The first stage (spermogonium stage) appears on the upper surfaces of the leaves or on young twigs as small bright-yellow or orange spots. Opposite these spots, usually on the under surface of the leaf, the cluster-cup stage appears, and it is similar in appearance to that of stem rust on barberries.

Distribution and economic importance.—Crown rust occurs generally throughout the oat-growing regions of the world. In the United States it is particularly destructive in the South, although, in certain years, it also may cause severe losses in the Northern States, especially near buckthorn bushes. In 1927 this rust destroyed 56,978,000 bushels of oats, amounting to 4.1 percent of the oat crop of the United States. Usually, in the Southern States, crown rust causes more damage than stem rust of oats, while in the Northern States the opposite is likely to be true.

Severe epidemics of crown rust may cause a 50-percent reduction in the yield of susceptible varieties of oats. In the immediate vicinity of rusted buckthorn bushes the oats may even fail to head, and the crop may be a total loss. The amount of damage depends on the susceptibility of the varieties grown and on the earliness and severity of the infection.

Life history.—The life history of crown rust is very similar to that of stem rust except that the cluster-cup stage develops on buckthorns instead of on barberries. In the Northern States the red or summer stage does not overwinter commonly, and epidemics result from the development of the cluster-cup stage on buckthorns or from summer spores that may be blown in from the South. It is clear from extensive observations that destructive outbreaks in the Northern States

[8] *Puccinia coronata* Corda.

seldom occur except in the immediate vicinity of buckthorn bushes, which are very numerous in certain areas. In the Southern States, on the other hand, the summer stage may persist throughout the year, and the rust there develops independently of buckthorns (fig. 7). How far north the summer stage will survive the winter in any given year depends on the amount of infection in the fall, and particularly on weather conditions during the winter. The rust develops on a number of wild grasses and, in the South, may survive the winter on them. In the North the existence of these grasses makes it relatively easy for the rust to spread from buckthorns to oats by way of the grasses, which often grow near the buckthorn bushes.

**Host plants.**—In addition to oats, more than 80 species of wild grasses may be attacked by one or another of several varieties of crown rust. Among the more common are quackgrass, reedgrass, redtop, meadow fescue, ryegrass, and bluegrass. These different varieties of rust vary in their ability to attack oats and the grasses. The variety of crown rust most prevalent on oats also attacks several grasses and a number of different kinds of buckthorn. The oat variety of crown rust comprises, in turn, a number of distinct parasitic strains that differ in their ability to attack different varieties of oats. Forty-two have been identified so far.

**Development of epidemics.**—Epidemics are most likely to develop when there are many spores in the spring and when weather conditions favor the development of the rust. In the winter-oat fields of the South, where the summer spores survive the winter, the rust gets an early start in the spring. The abundance of overwintering depends on the amount of infection in the previous season and on winter-weather conditions, mild winters being particularly favorable for the survival of the rust. In the Northern States, where the principal source of rust in the spring is the cluster-cup stage on the buckthorn, the amount of infection on these bushes will determine how early and how good a start the rust gets. If weather conditions in the early spring have been favorable for abundant infection on the buckthorns, there may be considerable crown rust if the subsequent weather conditions are also favorable. In occasional years summer spores may be blown into the Northern States from the South, and widespread epidemics will result. This, however, seems to occur rather rarely. Warm, moist weather is most favorable for the rapid development and spread of crown rust. It is quite probable also that the density of the stand is important. In dense stands moisture resulting from dews or rains is likely to be held longer, and there is better opportunity for the rust to develop than in thinner stands.

**Control.**—The cultural practices described for stem rust can be used to reduce the amount of crown rust somewhat, but they cannot prevent it entirely.

Some recently introduced varieties of oats, such as Victoria, Bond, and Alber, are highly resistant, but their general suitability for adoption still remains to be determined. Rainbow, Schoolmam, and similar Green Russian strains of economic importance also are more resistant than others.

Crown rust can be controlled by dusting with sulphur, but, as in the case of the other rusts, this method is too expensive to warrant its general adoption.

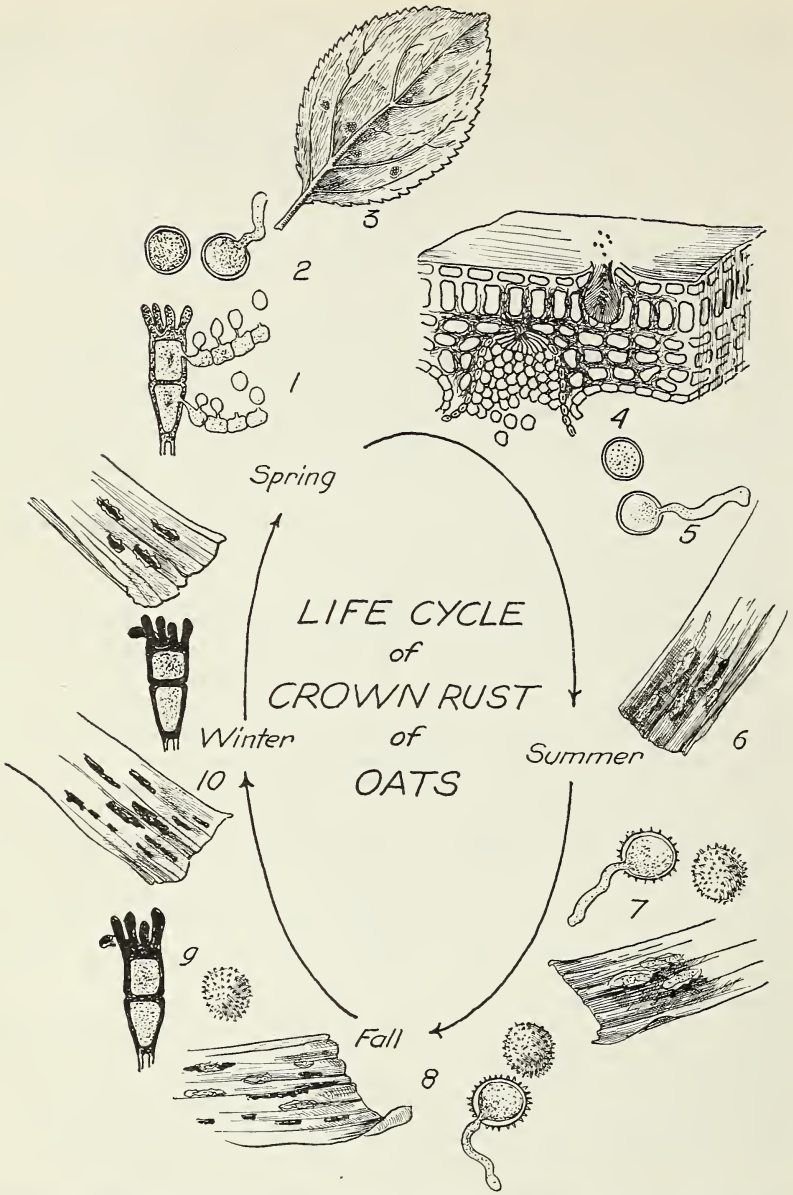


FIGURE 7.—Life cycle of crown rust of oats: Overwintering black spores (teliospores) (1) germinate in the spring and produce several very small spores (basidiospores) (2). If these spores lodge on the leaves of the buckthorn they will germinate there. The resulting infection of the buckthorn (3) produces spermogonia and cluster cups (aecia) (4). Cluster-cup spores (aeciospores) are blown to nearby oat fields, where they germinate (5) and infect the oat plants, causing the development of summer-spore pustules (uredia) (6) on the leaves and leaf sheaths. These pustules bear the summer spores (7), which reinfect the crop, producing more of their kind (8) until the infected plants begin to ripen, when the black spores (teliospores) (9) and (10) appear, mature, and spend the winter on infected-plant litter, where they germinate the following spring. In the winter-oat States summer spores may infect the fall-sown crop, and the rust may there overwinter and continue its existence without the intervention of the cluster-cup stage.

In the northern oat-growing States buckthorn bushes should be eradicated. It is just as important to destroy buckthorns to control crown rust as it is to destroy barberry to control stem rust. In many seasons the only destructive epidemics of crown rust in the Northern States occur near buckthorn bushes, and losses can be reduced greatly by eradicating them.

## BARLEY RUSTS

### STEM RUST[9]

**Description.**—The same as that for stem rust of wheat (p. 2).

**Life history.**—Barley is attacked by both the wheat and rye strains of stem rust; consequently, the rust from barley may attack all of the grasses that are attacked by the wheat and rye strains.

**Epidemiology.**—The factors affecting the development of the rust on barley are the same as those affecting the development of that on wheat.

**Control.**—Same as that for wheat stem rust (p. 7). Because of its relatively early maturity, barley is seldom so severely injured by stem rust as wheat. Nevertheless, in dense stands and in low places it may sometimes be injured. There are relatively few resistant varieties. Peatland, a variety developed at the Minnesota Agricultural Experiment Station, seems to be fairly resistant.

### LEAF RUST[10]

**Description.**—The pustules (uredia) of the summer stage of leaf rust of barley appear on the leaf blades and sheaths of the barley plant. They are yellow to yellowish brown, small, and round. The black stage follows the red stage and produces lead-gray pustules, which do not rupture the epidermis of the plant.

**Distribution and economic importance.**—Leaf rust of barley is seldom of any economic importance in areas where spring barley is grown. In those regions where winter barley is grown, however, it is sometimes destructive locally. At times it is so abundant as to prevent the proper heading of infected plants and may sometimes reduce the yields and the quality of the grain. From 1919 to 1927, inclusive, this rust destroyed 569,000 bushels of barley, an average annual loss of 63,000 bushels.

**Life history.**—The life history of leaf rust of barley is similar to that of the leaf rust of wheat. The spring or cluster-cup stage, when it is produced, develops on the star-of-Bethlehem, *Ornithogalum umbellatum* L., and a closely related species, *O. narbonense* L. (fig. 8). Although these plants are fairly common in certain parts of the United States, they rarely become rusted, and the rust survives the winters in the red or summer stage, as is the case with the leaf rust of wheat. It survives particularly in those regions where winter barley can be grown successfully.

**Plants attacked.**—Leaf rust appears restricted to cultivated varieties of barley, although under some conditions it may develop weakly on some of the other cereals and on several wild grasses. At least two parasitic strains of the rust organism have been found.

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[9] *Puccinia graminis tritici* Eriks. and Henn.
[10] *Puccinia anomala* Rostr.

**Control.**—The best method of controlling leaf rust of barley is to use resistant varieties. Certain strains of Coast, Luth, Oderbrucker, Turkestan, Chilean, Odessa, Peruvian, Quinn, Arequipa, Bolivian, Juliaca, Lynch, and Heil Hanna are very resistant. These have been crossed with other varieties, and hybrids have been obtained that may prove to be superior in resistance to any now grown.

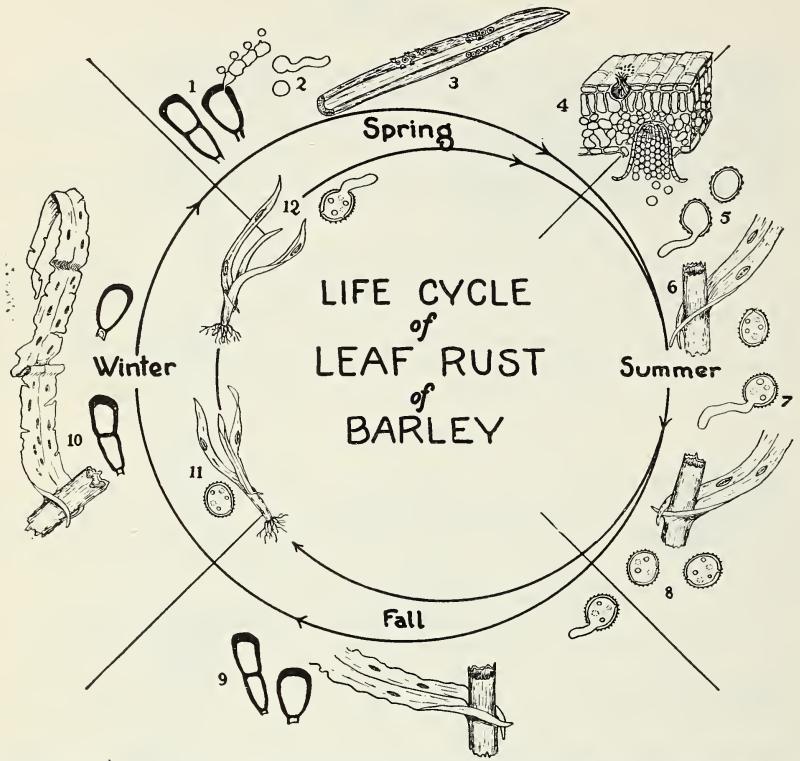


FIGURE 8.—Life cycle of leaf rust of barley: Overwintering black or winter spores (teliospores) germinate (1) in the spring, producing basidiospores, which, if they lodge upon star-of-Bethlehem plants, will germinate there and infect the leaves (2). The resulting infection (3) produces spermogonia and cluster cups (aecia) (4). Cluster-cup spores (aeciospores) find their way to growing barley plants and germinate (5). The resulting infection produces summer-spore pustules (uredia) (6) containing the summer spores (urediospores) (7), which may reinfect the barley, producing more uredia and urediospores (8), throughout the season, until the winter-spore pustules finally develop as the infected plants mature. The teliospores (9) thus produced live over winter on infected litter (10) and germinate in the spring (1). Where winter barley is grown, urediospores produced at harvest time (8) may infect volunteer barley plants and spread infection to the fall-sown crop. This infection (11) may survive and, with the return of favorable spring weather, produce uredia (12). Urediospores from these uredia reinfect the growing barley (6).

## RYE RUSTS

### STEM RUST[11]

**Description.**—The same as that for wheat stem rust (p. 2).

**Life history.**—Similar to that of wheat rust (p. 3). However, stem rust of rye attacks barley but does not develop on wheat and oats, except under specially favorable experimental conditions. In

[11] *Puccinia graminis secalis* Eriks. and Henn.

addition, it attacks, in general, the same grasses as does the variety of rust from wheat but, while the wheat rust does not commonly attack quackgrass, that grass is a congenial host for the rye rust.

**Epidemiology.**—The source of the stem rust of rye, in the spring, is almost exclusively the common barberry.

**Control.**—Because of the early maturity of rye and the fact that this crop is grown but little in the South, it is almost impossible to find severe attacks of stem rust on rye except where there are barberry bushes. No control measures except barberry eradication are required.

### LEAF RUST [12]

**Description.**—The leaf rust of rye usually attacks the leaf blades and sheaths, although it may occur also on the necks and glumes of severely rusted plants. The pustules of the red stage are scattered more or less irregularly and are orange-brown to dark cinnamon-brown. They are usually small but may unite to form fairly large pustules. The pustules of the black stage are similar to those of the leaf rust of wheat and leaf rust of barley. They are lead-gray to black and remain covered by the epidermis until it decays or falls away. Leaf rust of rye is very similar to leaf rust of wheat and was at one time included under the same name; but it is now known as *Puccinia dispersa.*

**Distribution and economic importance.**—The leaf rust of rye may occur wherever rye is grown. In the South, where rye is sometimes used for winter pasturage, it may become so abundant as to kill the plants during the winter. In the northern rye-growing regions it may also cause considerable losses. During the 9-year period 1919–27 leaf rust of rye destroyed 1,305,000 bushels, an average annual loss of 145,000 bushels.

**Life history.**—The life history of the leaf rust of rye is similar to that of the leaf rust of wheat. The spring or cluster-cup stage can develop on certain plants belonging to the borage family, but it is seldom found in nature in the United States and is, therefore, of no importance in the life history of the rust. The rust persists during the winter in the red or summer (uredial) stage and is, therefore, independent of the alternate host (fig. 9).

**Plants attacked.**—Leaf rust of rye produces its uredial and telial stages on cultivated rye and on *Secale montanum* Guss., a wild species of rye. While certain wild grasses may occasionally become infected under very favorable conditions, the rust generally is restricted to rye.

**Parasitic strains.**—This rust is so similar in many respects to the leaf rusts of wheat, quackgrass, bromegrass, etc., that it is sometimes considered as belonging to the same species but, as it is restricted to rye and produces its cluster cups on different plants, it seems preferable to consider it a distinct species. There is some evidence that there are parasitic strains of the rye rust that differ in their parasitic effect on inbred lines of rye.

**Development of epidemics.**—The development of epidemics occurs under conditions similar to those that promote epidemics of leaf rust of wheat. The degree to which the summer stage persists during

[12] *Puccinia dispersa* Eriks. and Henn.

the winter depends on weather conditions. In the spring, new infections occur and, if the weather is warm and humid, the rust may become epidemic. Rainy weather or cool, dewy nights and warm, humid days are most favorable for the development of the rust.

**Control.**—The cultural practices recommended in the case of stem rust, to the extent that they are applicable, may reduce somewhat the amount of leaf rust of rye. The rust could be controlled by dusting with sulphur, but the results probably would not justify the expense.

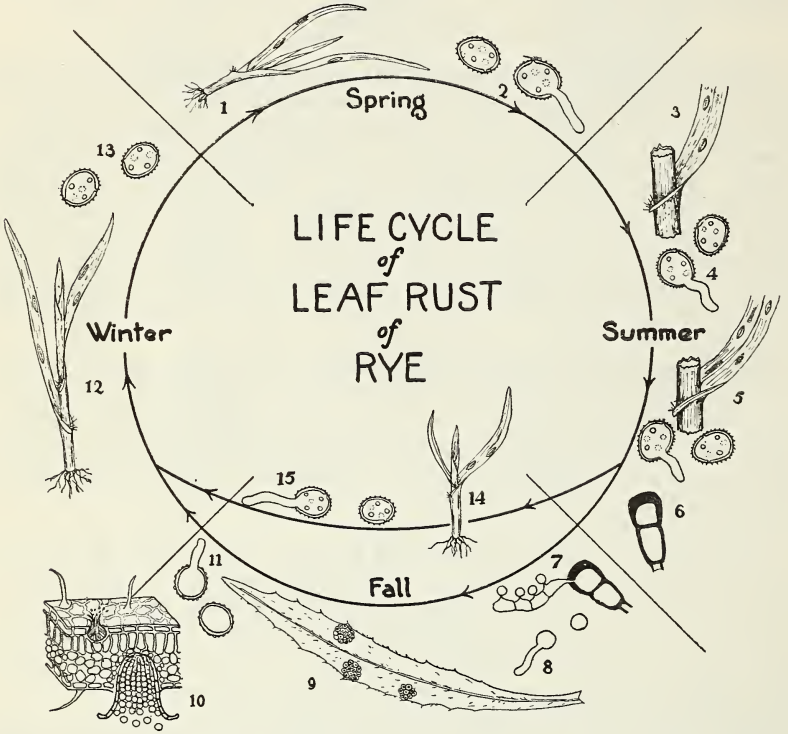


FIGURE 9.—Life cycle of the leaf rust of rye: Summer-spore pustules (uredia) (1) appear on rye plants in the spring, produce summer spores (urediospores) (2), which germinate and reinfect the growing rye, producing uredia (3) and urediospores (4). Reinfection continues (5) until finally, at harvest time, the black spores (teliospores) (6) are produced. In the late summer or early fall the teliospores germinate (7), producing basidiospores, which germinate (8) on species of alkanet (*Anchusa*) (9), where are produced the spermogonia and cluster cups (aecia) (10). The cluster-cup spores (aeciospores) may lodge on volunteer or fall-sown rye, germinate there, and produce uredia (12) or mycelium. In this way the rust fungus survives the winter and, with the return of favorable spring weather, produces urediospores (13), which may reinfect the developing rye (1). Urediospores produced at harvest time (5) may infect volunteer rye (14) and produce urediospores (15), which may infect fall-sown rye (12).

No variety of rye has been found that is uniformly highly resistant to leaf rust. This is to be expected, as rye is mostly cross-pollinated, and it is difficult to maintain varieties in their original purity. There are, however, resistant and susceptible individuals in most varieties of rye, and it has been possible by means of inbreeding to select a few self-fertile strains that are highly resistant to leaf rust. These inbred strains, however, are not vigorous, and

further crossing will be necessary before commercially valuable resistant varieties can be developed.

### CORN (MAIZE) RUST[13]

**Description.**—Corn rust attacks all types of corn, including dent, flint, pop, and sweet varieties. The uredia are cinnamon-brown and the telia are brownish black.

**Distribution and economic importance.**—Corn rust is found wherever corn is grown, but it is most destructive in regions of high humidity, as in the Corn Belt and in the South Atlantic and Gulf States. While statistics regarding its destructiveness are meager, it may severely affect very susceptible varieties. This rust caused a total reduction of yield of 25,124,000 bushels from 1917 to 1927, inclusive, or an average annual loss of 2,284,000 bushels.

**Life history.**—The cluster-cup stage may be produced on several species of woodsorrel (*Oxalis*). The black stage survives the winter on infected corn litter and infects the *Oxalis* plants in the spring. From these infected plants the rust may then spread to corn (fig. 10). The red or summer stage may possibly persist to a certain extent on corn leaves or corn stalks in certain regions and infect corn directly the following spring. Warm, moist weather seems most favorable for the rapid development of this rust.

**Parasitic strains.**—There are several parasitic strains of the corn rust which differ in their ability to attack varieties or inbred lines of corn. It is probable that these may have originated by hybridization between existing strains on *Oxalis*, the alternate host.

**Control.**—Corn is cross-pollinated and there is, therefore, considerable variation in the susceptibility of commercial varieties to rust. Some of them are very susceptible, others moderately so, and some are highly resistant. In the regular program of corn improvement now being carried on, rust is taken into consideration, and it seems probable that resistant strains possessing other desirable characters also can be obtained.

### SORGHUM RUST[14]

**Description.**—The rust of sorghum occurs on sorghum, Sudan grass, and Johnson grass and may be found on other related grasses. On these plants the uredial and the telial stages of the rust may be found, largely confined to the leaves and leaf sheaths of the plant. The uredia are chestnut-brown, fairly large and oblong, and usually surrounded by a zone of purple tissue. Pustules of the winter stage are chocolate-brown. No alternate host for this rust has yet been discovered.

**Distribution and economic importance.**—In the United States the rust of sorghum occurs to some extent in the Southern States and may be found occasionally as far north as Indiana and Kansas.

Although some varieties often are very heavily rusted, little is known concerning the effect of this rust on yield. Different varie-

[13] *Puccinia sorghi* Schw.
[14] *Puccinia purpurea* Cooke.

ties show marked differences in reaction to this rust. The milos, a line of Dwarf Shantung kaoliang, and a line of shallu have thus far shown marked resistance. Blackhull and Reed are moderately

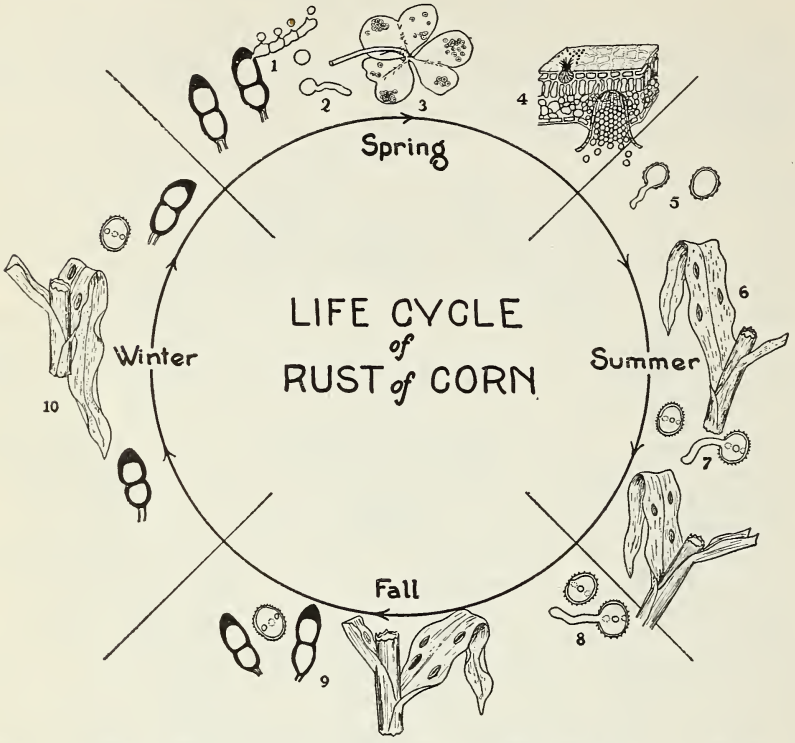


FIGURE 10.—Life cycle of the rust of corn: Overwintering black spores (teliospores) (1) germinate in the spring and produce basidiospores (2), which may germinate on *Oxalis* (sorrel) plants (3). The resulting infection of the *Oxalis* leaves produces spermogonia and cluster cups (aecia) (4). The cluster-cup spores (aeciospores) produced on *Oxalis* may find their way to corn plants and germinate on the leaves (5). The resultant infection produces summer-spore pustles (uredia) (6) and summer spores (urediospores) (7). These spores germinate on corn and produce more urediospores. This process is repeated several times during the summer and early fall. In the fall, black-spore pustules (telia) (9) and teliospores more or less replace the uredia and urediospores. The teliospores survive the winter (10) on corn litter and germinate in the spring (1). There is some evidence that a few urediospores may occasionally remain viable in protected situations, such as the interior of corn shocks. It is possible that these may occasionally infect young corn in the spring.

resistant. Completely susceptible, on the other hand, are the feteritas, Dwarf Sumac, Fielding Sumac, and Red Amber, kafir, and Sunrise. Leoti Red, Freed, White African, Kansas Orange, and Dawn are moderately susceptible.

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